

Upon the Development of the Enamel in Certain Osseous Fish

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II.—Upon the Development of the Enamel in Certain Osseous Fish.

By Charles S. Tomes, M.A., F.R.S.

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[PLATE 5.]

The development of the enamel in Placental Mammals has always proved a difficult subject for investigation, principally because the change from the unaltered formative cell or ameloblast into the perfected enamel prism is so abrupt that the intermediate stage occupies only an exceedingly narrow zone. Indeed, many observers have supposed that the ameloblast cell undergoes a direct conversion into an enamel, without practically any intermediate transformation, whilst others have supposed that it secreted and shed out from its free end the material of which an enamel prism is composed, namely, an almost crystalline mass of calcium salts with a mere minute trace of organic substance. In a paper recently published in the 'Philosophical Transactions' (8), I showed that in the Implacental Mammals, in which the ultimate enamel contains a tube system, the transition from the unaltered ameloblast to the finished enamel was more gradual, and that it was possible to follow the steps of the process more satisfactorily owing to the persistence, for a time, in the forming enamel of conspicuous organic structures of definite form and arrangement. opinion the two processes are not essentially different, and that which is easily seen in the marsupial may be used to elucidate that which is only with difficulty traceable in the placental group.

But in a subsequent investigation into the formation of enamel in the Plagiostome fishes (9) I found an essential, and, indeed, an almost radical, difference, for in them the tissue which has generally been termed enamel is deposited in a thick and complete organic matrix, which presents the striking peculiarity of being furnished by the mesoblastic dentine papilla, and the claim of the tissue to be called enamel rests partly upon the immense development of the ameloblasts over it during the period of its calcification. This matrix is laid down of the full thickness of the ultimate enamel before any calcification in it takes place, and calcification is exceedingly rapid.

This suggested a search amongst other fish, with a view of finding if there were any methods of enamel formation which would serve to bridge over this wide difference observed between the plagiostomes and mammals; in the former the F 2 13.6.1900.

enamel being a joint product of a mesoblastic papilla and an epiblastic enamel organ, while in the latter the whole work is done by the epiblastic ameloblasts. The most promising field for inquiry appeared to be amongst those fish enamels which differ most in their structure from mammalian or reptilian enamels, especially as some of them happen to present certain slight resemblances to Plagiostome enamels in structure.

Such are the enamels of the Sheep's-head fish (Sargus ovis, Plate 5, fig. 12) and of the Wrasse (Labrus), which present an appearance of strongly-marked striæ which run in from the free surface, and changing their direction and at the same time becoming finer and less distinct, are lost completely before they reach the dentine surface (12). It is generally believed that these markings are due to the existence of a set of tubes, but some uncertainty rests upon this (1); in any case they are totally different from the tubes in marsupial enamel, which run from the dentine, with the tubes of which they are continuous; that is to say, in the opposite direction. But I soon found that the difficulty of making satisfactory preparations of these tooth germs was almost insuperable; they lie deep in the bone, completely enclosed in their crypts, so that the various fixing agents employed fail to reach them with sufficient freedom to protect the soft tissues from damage during decalcification and other subsequent Hence, although the preparations, read by the light of more perfect ones obtained elsewhere, threw light upon their process of enamel formation, they were not sufficiently good to serve for a close investigation, and I had to seek for some other fish in which these adverse conditions did not prevail, and finally resorted to certain of the Gadidæ, principally to the Ling and the Hake.

In all of the Gadidæ the teeth are surmounted by sharp caps of enamel which sit like spear-points upon their apices (10); and, in favourable sections, the enamel is marked by a fine striation which runs in from the free surface and recalls the structure seen in greater perfection in *Sargus* and in *Labrus*. (Plate 5, fig. 1.)

These caps are fitted on to a shoulder of the dentine which is hollowed out into a circumferential groove, so that, although the enamel cap is of material thickness, it does not greatly increase the outside dimensions of the tooth. Whether the enamel is confined to this cap or is continued down over the rest of the tooth is a matter which becomes of some interest when the enamel organ of the tooth germ is considered; it might seem to be a very easy point to determine, but as a matter of fact it is very difficult to be quite certain whether there is or is not an exceedingly thin layer of distinct material surrounding a ground section of any somewhat highly refractive substance, for optical effects due to the thickness of the section often very closely simulate the existence of such a layer where none actually exists. As, however, there is some appearance of an exceedingly thin layer which is more brittle than the rest of the tooth, all that can safely be said is, that if there be any enamel over the sides of the tooth it is not more than 10μ in thickness, *i.e.*, is exceedingly rudimentary. When subjected to the

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action of an acid, the whole enamel cap quickly dissolves away, leaving only a mere trace of organic residue, so that in the finished condition the enamel can contain but a very small percentage of organic matter.

In its earliest stages the tooth germ of the Hake or of the Ling does not present any marked peculiarities, and resembles a mammalian tooth germ; at a period immediately antecedent to the commencement of dentine calcification the dentine papilla (186 μ in length) has a sharply-defined border, beneath which, and apparently not quite reaching up to it, is a well-defined layer of odontoblast cells averaging 18 μ in length. (Fig. 2.)

Enclosing this like a cap is an enamel organ which consists of the usual double row of cells, the inner of which (ameloblasts) form the internal epithelium of the enamel organ, and are elongated columnar cells 19 μ in length. They only differ slightly from the ordinary type of ameloblast in that their plasm stains somewhat freely and in that their nuclei are, even at this early period, not so distinct.

Towards the base of the dentine germ the ameloblasts become less elongated, and pass by gradual transitions into the reflected second or outer layer, which forms the external epithelium of the enamel organ, and consists of rounded cells. These two layers of cells are everywhere in contact, save where an obviously accidental space occurs; hence there is no stellate reticulum formed between them.

A fairly well-defined tooth sac which, as usual, is formed by a condensation of the surrounding connective tissue, envelops the tooth germ.

At the next stage which it is necessary to describe, a very thin shell of dentine has calcified, and the tooth sac has greatly increased in size; the dentine pulp, which is of course attached at its base, has not fully participated in this activity of growth, so that there is a large amount of space left above it between its apex and the inner wall of the tooth sac, and here the peculiarity of the process of enamel formation begins to be apparent. (Fig. 3.)

The space above the top and sides of the dentine germ is occupied by a delicate tissue, which has a reticulated appearance, and reaches quite out to the wall of the tooth sac, thus occupying the position of an enamel organ. But in it none of the usual constituents of an enamel organ can be recognised; there are no ameloblasts, no stellate reticulum, nor external epithelium of the enamel organ, but in their place, and in the position but a short time before occupied by the ameloblasts, is this reticulated stroma. No such tissue exists at any time during the formation of mammalian enamel.

Hence it is necessary to examine it and its relations with some care, especially as no such manner of enamel formation has hitherto been described.

Although the teeth of the Hake vary in size not only according to the dimensions of the fish, but also in different parts of the mouth of the same fish, so that it is not possible to predict what sized tooth would ultimately be produced by a given tooth germ, yet the examination of a large number of teeth shows that the proportion

between the length and width of the entire tooth and that of the length and width of its enamel cap is fairly constant. And in the tooth germ, when once a skin of dentine is calcified, we get a measure of the width of the dentine at the level of the shoulder, and also of the length of the pointed apex of the dentine which is contained within the enamel cap; and these dimensions will not be altered by any subsequent growth, as all the addition to the dentine takes place on its interior. A large finished tooth measured 6.3 mm. in length; its enamel cap was 738 μ in length, and the dentine at the shoulder was 300 μ in width, and entered the enamel cap for a distance of 330 μ . Now the width of the dentine cap at the shoulder in the tooth germ figured (fig. 3) very nearly corresponds to the above-given measurements of a completed tooth, so that it is fair to assume that the enamel cap would, when formed, have been about 730 μ in length.

As a matter of fact, the distance from the shoulder to the interior of the tooth sac above it is 670 μ , this space being occupied by the reticulated stroma before alluded to. Hence it is fair to say that, even at this early period, when little enamel has yet been formed, the reticulated stroma has attained to the full ultimate dimensions of the enamel cap. In other words, in place of the enamel being manufactured by the ameloblasts, so to speak, from hand to mouth as in mammals, a preparation is made for it by the development of an organic stroma of its full dimensions, the correspondence in measurements being quite as close as could be expected in a much manipulated decalcified section.

Thus, the stroma into which the ameloblasts become transformed is exceedingly thick over the area where enamel is to be formed, but the enamel organ is continued down below the shoulder, tapering down almost to a thin edge when it reaches the base of the dentine papilla; towards this point it has still the appearance of unaltered ameloblasts. The enamel organ is, however, coextensive with the dentine papilla, even where no enamel or only a partial investment will be formed (2 and 12, pp. 372, 128). From the existence of a sharply-marked shoulder in the thin skin of dentine, it would seem probable that some enamel had already been formed; but as the section has necessarily been decalcified, not much is to be seen of it.

But in a few sections a thin film of material which has taken a stain faintly is found in the position of the enamel cap, whilst in other sections a certain amount of space which intervenes between the well-marked reticulated stroma and the formed dentine is occupied by a transparent, and apparently homogeneous, material, which is only rendered apparent by its having in places slightly parted from the dentine and having become crinkled at its edge. (Fig. 3.) Thus at a very early period, when the dentine cap is only about 18 μ in thickness, enamel of much greater thickness, i.e., about 90 μ , has already been more or less completely formed; this is a reversal of the order of procedure obtaining in mammals, in whom the dentine always antedates the enamel considerably. This inference is borne out by appearances found in sections which have not been decalcified. If small round tooth sacs are carefully picked out of

the mucous membrane between the bases of the completed teeth and stained, they can be imbedded and cut without decalcification. Of course this usually involves some displacement of the parts, but sometimes in fortunate sections things remain almost in situ, and even when they do not, by comparison of many sections the original disposition can be made out. Such sections prove incontestably that the formed enamel at an early stage is three or four times as thick as the dentine, and the thickness of the formed enamel, plus the thickness of the as yet uncalcified stroma, makes up the calculated future thickness of the enamel for the particular tooth. (Fig. 4.)

This enamel is perfectly translucent and shows little structure, save that its manner of splintering at its edge indicates that it is built up of prisms. Its outermost layer, *i.e.*, its youngest portion, is defined by its taking stains very deeply; there is also a region of very deep staining where the enamel meets the dentine, the latter, as might be expected in a section not decalcified, taking the stain but faintly; though in decalcified sections the collagen matrix takes stains strongly. In those sections cut without decalcification the stroma of the enamel organ seems to stain somewhat more readily than in those which have been subjected to the action of acid, but otherwise there is little difference to be made out in its appearance; hence it may be concluded that in the decalcified specimens this reticulate stroma had not as yet received any material impregnation with lime salts. (Fig. 5.)

This stroma has a general appearance of fibrillation in a direction at right angles to the dentine surface, and it is not altogether unlike a fine-meshed connective tissue, but no cells such as the connective tissue corpuscles are to be seen in it. already been repeatedly mentioned, it is reticulated, the meshes showing elongation to a considerable length in some sections, whilst in others they are nearly round. These differences are probably wholly due to the plane in which it happens to be cut; when the section is on a plane pretty truly at right angles to the dentine surface, the meshes are very greatly elongated, and when it approaches to parallelism with the dentine they are round or hexagonal. In fact, the appearances are not very different from those which would result from the apposition of a number of thin-walled tubes running perpendicularly through it with delicate walls, and, perhaps, some interstitial substance, a sort of honeycomb with enormously elongated cells; as, however, they do not pursue an absolutely straight course, the whole length of any particular mesh never lies within a single section. It takes even plasm stains only feebly, hæmalum staining it better than most other stains, but its outermost portion always stains much more deeply than the rest, and rounded forms are there seen which at first I was inclined to regard as nuclei, the nuclei of the transformed ameloblast cells. But in sections which lie at right angles to the long axis of the tooth germ, and therefore cut this region into slices nearly parallel with its own surface, it is found that though the stained areas are circular, their outer borders are indefinite, and that they surround sharply-defined circular areas which are less deeply, or not at all, stained; this seems to negative the idea of the stained spots seen in longitudinal

section being really nuclei. And in following a series of such consecutive sections which lie deeper and deeper in the stroma, the stained areas gradually disappear, but the sharply-bordered circles which they surround remain. A cross section some distance within the stroma shows nothing but circular areas, lying separated from one another, and with a delicately striated tissue intervening between them. (Fig. 6.) The rings vary from 3 μ to 5.5 μ in diameter, and the spaces between them vary much in size; in the outer portion, where the stained areas surround them, these latter are about 8 μ in diameter. When the section is oblique, the rings become ovals, sometimes much elongated, so that they appear to be sections of either tubes or rods of considerable length. Again, in sections in which the rings are circular and without stained areas surrounding them, there seems to be occasionally a marking out into polygonal areas, in the centres of which lie the rings.

In longitudinal sections dark bodies, more or less oval, occur; but on alteration of focus these become transformed into clear areas with sharp borders, so that they are probably nothing but the rods or tubes above alluded to, only seen out of focus. (Fig. 5.)

The exact mode by which the ameloblasts of a very young germ become transformed into this reticular stroma is not easy to follow; the ameloblasts at first increase greatly in length, without losing their individuality, and then their nuclei become much less conspicuous.

But, notwithstanding the examination of a large number of sections prepared in different ways, I have failed to satisfy myself as to whether the ameloblast cell itself goes to form the rods or tubes of the stroma, the interstitial material being formed outside and between them; or whether the whole cell, so to speak, breaks up, and the resultant reticular structure is thus altogether cellular in origin.

Thus the same doubt rests upon its development that exists in the case of connective tissue elsewhere, it being still uncertain whether the fibres of connective tissue which constitute its reticulum are formed between or out of the substance of cells. This stroma is peculiar in that it is formed from epithelial cells of well-marked character, but a partial analogy may be found in the enamel organs of mammals in which the stellate reticulum of the enamel organ is derived from the same mass of epithelial cells which form the ameloblasts and the external epithelium of the enamel organ, though here again there is doubt as to the precise method in which their transformation into a stellate reticulum takes place (14). As, however, the mammalian enamel organ at the antecedent stage consists of a solid mass of cells enclosed by a layer in which the cells are somewhat more differentiated, there is nothing besides cells there, and so the whole of the stellate reticulum, directly or indirectly, must proceed from them.

So far, then, the stroma has been shown to consist of two elements, the sharply-defined tubes or rods and a delicately-fibrillated tissue which intervenes between them, both alike being arranged in a direction generally perpendicular to the dentine

surface. And it is clear that impregnation with lime salts has not at this period gone on to any extent, for the appearances presented by sections of decalcified material and those cut without decalcification differ but very little; the slight difference in the ease with which they stain being perhaps due to some residual acidity in the former.

But while this stroma reaches very nearly up to the surface of the formed enamel, and presents no material difference in its appearance in this region, and at the point farthest from the enamel surface, yet quite close to the formed enamel the rods or tubes are not to be seen, and there is only a delicate meshwork. (Figs. 5 and 9.)

Naturally this is best seen in decalcified sections cut in paraffin, but it may be also traced in sections cut without decalcification, and it suggests the idea that here the impregnation with lime salts has gone so far as to obliterate the organic structure almost wholly, leaving only a trace of it between the prisms formed.

It is a curious and rather unaccountable feature common to all enamel development that whilst there is organic material present close to the line of calcification in some abundance, there is very little organic matter present in the finished tissue (11 and 14), far less indeed than has usually been believed, water of crystallisation having been computed in most analyses as organic matter, because it disappears on ignition of the previously dried material (11). How the organic basis which was present up to the last moment is got rid of is an unsolved problem. But although 1 or 2 per cent. of organic matter is enough to leave a very appreciable residue after solution of the lime salts by an acid, and, if brought into solution, is amply sufficient to give clear proteid reactions, no such evidence of its presence can be obtained from enamel.

Another peculiarity in the enamel development of the Gadidæ is that, after the transformation of the ameloblasts into the stroma, there are no conspicuous cells to which can be assigned the function of separating out the lime salts, a function which is apparently discharged by the ameloblasts in mammalian tooth germs.

Immediately outside the stroma and in the walls of the tooth sac is an abundant plexus of vessels, which thus lie practically in contact with the stroma, but they do not enter it, nor are there any large cells in relation with these vessels, so that one is driven to the conclusion that, the stroma once formed, it is able to draw into itself the required lime salts, and to deposit them at that point which is farthest from the vessels.

This deposition of lime salts at the points most distant from the vessels, and even at a little distance from cells, is not, however, unusual, for as has been pointed out by Professor Sims Woodhead (15), this is exactly what generally takes place in calcifications elsewhere. And it is what happens, though at a point much less remote, in the calcification of a mammalian ameloblast, which undergoes calcification at its distal extremity, these cells being themselves yet further separated from the vessels by the interposition of the cells of the stratum intermedium and of the external epithelium of the enamel organ.

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To revert to the rods or tubes which have been described and figured (figs. 5, 8), it seems hardly possible to doubt that they bear some relation to the forming prisms, and are a stage in their development, and the fact that they are not to be distinguished in that portion of the enamel stroma which lies close to the dentine tends to bear out this view. For it is to be remembered that the marked striation of the finished enamel, whether it be due to tubes or to very distinct prisms, does not exist in the inner portions which lie close to the dentine; this may be better seen in the thick enamel of *Sargus* than in the comparatively scanty enamel of the Gadidæ, though it is true of both alike.

But whether the appearances figured are sections of solid rods or of tubes remains uncertain. The substance, if any, which lies inside the sharply-cut rings will not stain with any stain which I have employed; but this does not prove that there is nothing there, and even under the highest powers there is no appearance of double contour in the rings, which one might have expected to see were they tubes with a bounding wall.

One is tempted to compare them with the long fibrillar processes which run through the developing enamel of Marsupials (8); but it must be remembered that these have been shown to be prolongations of the plasm of the ameloblast cells, whereas no such relation can be established in the case of these bodies seen in the Gadidæ, as they are not seen prior to the disappearance of these cells.

Two facts are perfectly clear: the first, that the enamel of these fishes is certainly not an excretion from the end of the ameloblasts, for they have disappeared long before calcification takes place; the other that the calcification does take place in the form of a conversion of or a deposition in a pre-existent stroma of definite arrangement.

My preparations of *Sargus* and of *Labrus*, though less perfect, amply suffice to prove that in these fishes there is a bulky enamel stroma of similar character to that here described; in fact, that the process is in all essentials the same as in the Gadidæ.

And, as has already been mentioned, all these fish have enamels which possess a character not met with in mammalian enamels, namely, a distinct striation which starts inwards from the free surface, and is lost before it reaches the dentine surface, and in all it remains somewhat doubtful whether these striæ are tubes or merely very distinctly marked-out solid prisms which serve to make this peculiar and characteristic pattern. I have never been successful in getting coloured fluids to enter the striæ of these enamels, but this does not quite disprove their being tubes, for their orifices may have become blocked up during the use of the tooth, or they may be occupied by the dried remains of uncalcified material (1 and 12, p. 36).

Conclusions.

Notwithstanding that the completed enamels of Plagiostome fish, of Osseous fishes, of Marsupials, and of Placental mammals, present resemblances which are far stronger

than their differences, whether chemical, physical, or histological, it must be taken as established that the formative process is by no means identical in the different groups.

And it seems a fair inference that these differences may represent stages in the evolution of enamel; at all events, we are now in a position to divide enamels into groups based upon the method of their development. First must be placed the enamels of Plagiostome fishes, which may be thus briefly characterised:—

A. Enamel which is not wholly Epiblastic in Origin.

This is laid down in a pre-existent matrix derived from the outermost portion of the dentine papilla, the surface of which undergoes a special transformation, and is of the full thickness of the ultimate enamel. The ameloblasts, however, participate in the process, as is shown by their enormous development over the area, and by their immediate atrophy when enamel formation is accomplished. This is met with only, so far as is known, in Plagiostome fishes, and stands in a measure apart from the other methods (9).

B. Enamels wholly Epiblastic in Origin.

- 1. The ameloblasts speedily lose their integrity and become transformed into a stroma of definite structure and of the full dimensions of the ultimate enamel. In this stroma calcification goes on, proceeding outwards from the dentine surface, and is so complete that very little organic residue is found in the finished tissue; it is also very rapid, so that the enamel is more advanced than the dentine. This process is found in all of the Gadidæ, in *Labrus*, and in *Sargus*; probably also in many fish.
- 2. The ameloblasts persist and retain their characters throughout the whole period of enamel formation, and are not bodily transformed into an enamel stroma. Their free ends, however, are continued into long fibrillar processes (exaggerated Tomes's processes) which, while enamel formation is actively going on, can be traced through a great part of its thickness. This method has only been found so far in Marsupials, though it is probable that it may be common to tubular enamels; such are found in Hyrax, Jerboa, the Shrews, &c. (8).
- 3. The ameloblasts persist throughout the period of enamel formation, and retain their characters. Their free ends are produced into short processes (Tomes's processes) which dip only a little way into the young enamel; the full calcification follows very close upon the heels of any alteration of the ameloblasts, so that there is only a very narrow zone between the unaltered ameloblast cell and perfect enamel (3, 4, 6, 13, 14). This is found in the vast majority of Placental mammals.

A comparison of the several methods above enumerated seems to indicate an increasing specialisation in the ameloblast cells, and an increasing importance in the part played by them. Although in the first (A) it would appear as though they took little

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part in the modelling of the tissue, and perhaps only served to segregate the lime salts required for it, yet in the Rays, in whom the finished product more nearly resembles a mammalian enamel, the specialised outer layer of the dentine papilla is less strongly marked than in the Sharks.

In the second (B, 1), the ameloblasts absolutely lose their individuality, but, inasmuch as they are themselves transformed into the stroma, which is the site of enamel calcification, they must be credited with its entire production.

In the third method (B, 2) their free or working ends alone are transformed into a fibrillar tissue, the cell retaining its integrity, and each cell forming the whole length of a particular enamel prism.

In the fourth (B, 3) a precisely analogous process goes on, but the transformation of the cell into any form of intermediate tissue occurs only at the last moment, so that it is easily overlooked.

The four methods hence by no means present a complete gradation of the one into the other, such as might be expected when we consider the simplicity of the structure of all enamels, and their close similarity in physical and chemical characteristics. There are important gaps in the chain, and it is probable that links exist which have yet to be described. Yet I have thought it better to publish the results of my inquiry, so far as they go, in the hope that they throw some light upon the matter. But the last word has by no means been said upon the subject of enamel, or indeed of any other calcification, and it may be long before it is. For the inherent difficulties of investigation in a region where very hard and very destructible elements lie in close juxtaposition must always remain great.

The literature which has any immediate bearing upon the subject-matter of this paper is singularly scanty; although the development of the enamel in man and in Placental mammals has been much studied, I have not been successful in finding much that relates to that of fish. Röse's paper, referred to in the list of references (5), does not enter into the calcification of the tooth germs at any length, and refers chiefly to the early stages of their formation; moreover, he has only examined those of the Salmonidæ amongst osseous fish. And the important paper of Richard Semon (7) upon the development of the teeth of Ceratodus, which seems to fully establish the interesting point that the dental plates of this fish are formed by the concrescence of many originally distinct tooth germs, contains nothing which bears upon enamel development; but it is to be desired that those who may possess the material should investigate the enamel formation of Dipnoi, as it is very possible that they might present some transitional stage, at present unknown.

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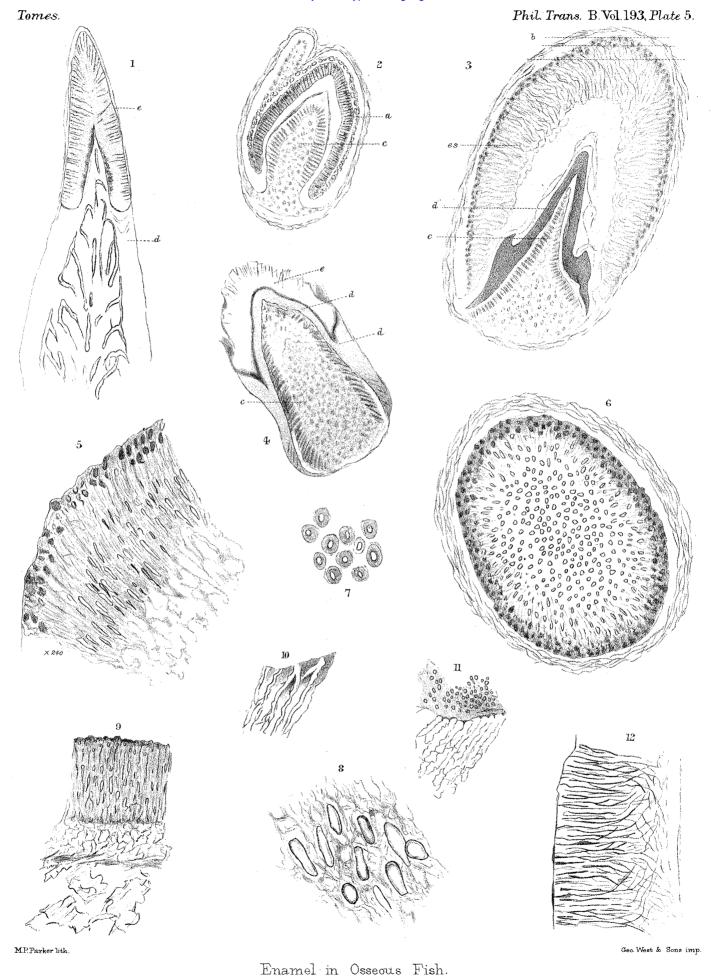
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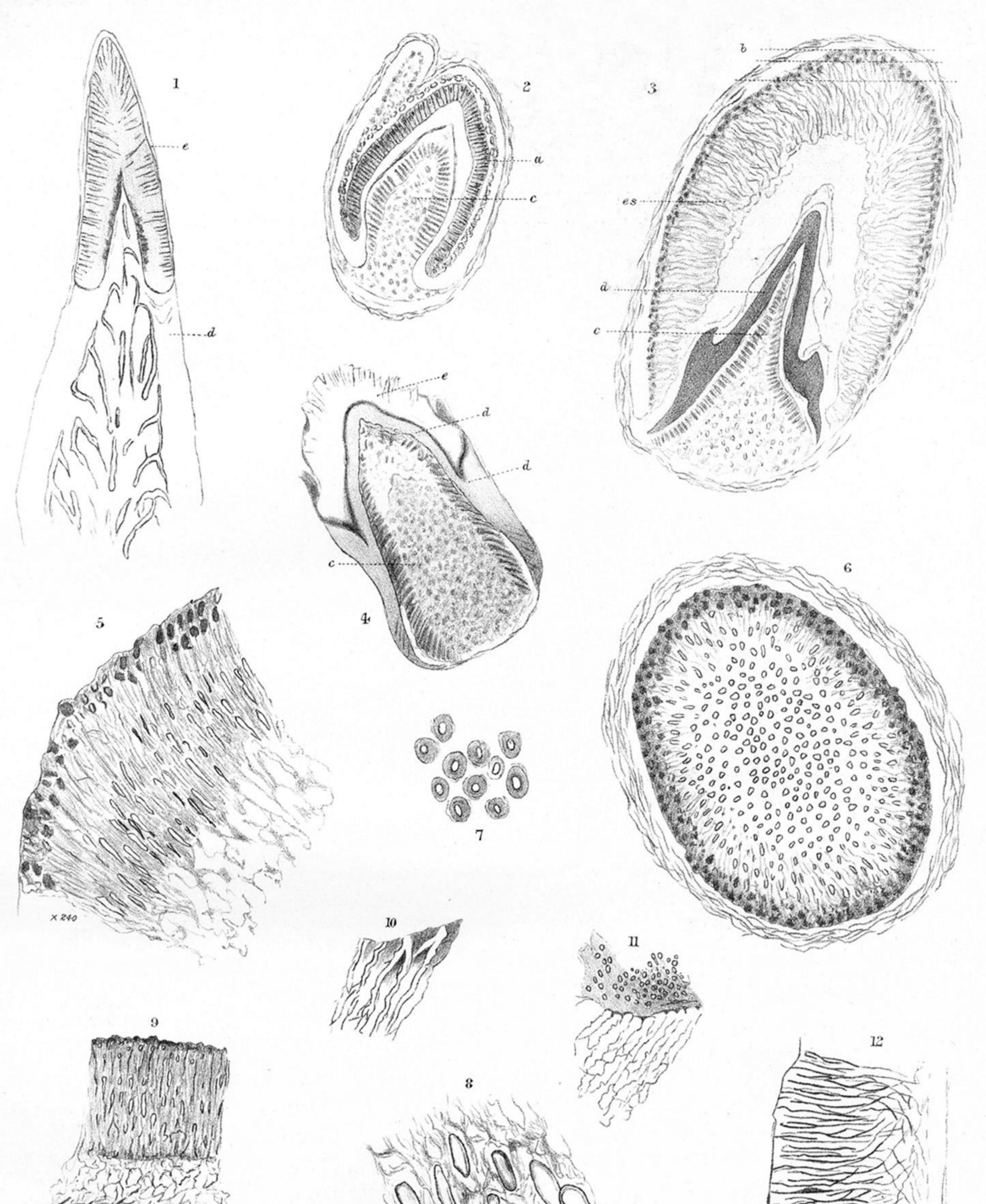
DESCRIPTION OF PLATE 5.

- a. Ameloblasts.
- b. Stained outer border of enamel stroma.
- c. Dentine papilla.
- d. Formed dentine.
- e. Enamel.
- e*. Decalcified residue of enamel.
- es. Enamel stroma.
- f. Wrinkled edge of (?) decalcified enamel.
- Fig. 1. Longitudinal ground section of apex of the tooth of a Hake (*Merlucius*), showing the cap of enamel (a) fitted on to a shoulder of dentine (d). \times 80.
- Fig. 2. Longitudinal section of a tooth germ, prior to the commencement of any calcification. The ameloblasts are not yet transformed, and are of the usual type. × 160.
- Fig. 3. A tooth germ in which a thin layer of dentine has already been calcified. The ameloblasts are no longer distinguishable, having been transformed into a reticulate stroma. Apparently enamel formation has gone on to a certain extent close to the dentine cap, where a structureless film with a folded edge is visible under careful illumination. × 140.

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- Fig. 4. A section of tooth germ cut without decalcification. The free edge of the enamel is splintered, and the boundary line between it and the dentine is dark, the section being deeply stained in this position. × 100.
- Fig. 5. Enamel stroma from a similar section cut without decalcification, deeply stained with hæmalum. Along its outer border are bodies not capable of being sharply defined, which have stained deeply; then follows a delicate reticulated tissue with distinct longitudinal general arrangement in which are seen oval clear spaces, while below and to the right it merges into a fainter and more open meshed tissue. × 240.
- Fig. 6. A section lying close to the exterior of the apex of a young tooth germ, and cut in a plane transverse to the long axis of the germ about in the position and in the plane of the third line across the top of fig. 3. The stained bodies of the exterior of the enamel stroma shown in figs. 3 and 5 are also seen in this, but inside them the whole space is filled up with sharply-bordered rings looking like tubes cut across. × 180.
- Fig. 7. Drawn from a portion of the same section near to its outer portion, though within that which is most deeply stained. The rings surround clear spaces, but these are themselves surrounded by stained areas, the outer edges of which cannot be sharply defined (the definition of the outer edges has been exaggerated in the figure). × 850.
- Fig. 8. Highly-magnified section of enamel stroma which is nearly longitudinal, the oval form of the sharply-defined areas being due to slight obliquity in the section; they lie in a delicate meshwork, and are the same things as the oval areas seen in fig. 5. × 1000.
- Fig. 9. Enamel stroma from a tooth germ in which some enamel has already been calcified. This section having been cut without decalcification, fragments of enamel lie at the bottom of the figure, and above them and between them and the unaltered stroma is a more open meshwork. × 180.
- Fig. 10. A portion of young enamel (not decalcified) showing an appearance of tubes traversing it. × 300.
- Fig. 11. A portion of enamel seen obliquely so that two surfaces are in view. On its upper surface an appearance of holes, recalling fig. 6, is seen, whilst below the side of the fragment is shown. × 240.
- Fig. 12. Enamel of Sheep's-head fish (Sargus) showing the appearance of lines (? tubes) running in from the free surface, and bending and branching till they become lost before reaching the dentine surface (to the right in the figure).



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Enamel in Osseous Fish.

DESCRIPTION OF PLATE 5.

Ameloblasts.

- b. Stained outer border of enamel stroma.
- c. Dentine papilla.d. Formed dentine.
- e. Enamel.
- *. Decalcified residue of enamel.
- es. Enamel stroma.
- Fig. 1. Longitudinal ground section of apex of the tooth of a Hake (Merlucius),

Wrinkled edge of (?) decalcified enamel.

- showing the cap of enamel (a) fitted on to a shoulder of dentine (d). × 80.

 Fig. 2. Longitudinal section of a tooth germ, prior to the commencement of any calcification. The ameloblasts are not yet transformed, and are of the usual
- type. × 160.

 Fig. 3. A tooth germ in which a thin layer of dentine has already been calcified.

 The ameloblasts are no longer distinguishable, having been transformed into a reticulate stroma. Apparently enamel formation has gone on to a certain
- extent close to the dentine cap, where a structureless film with a folded edge is visible under careful illumination. × 140.

 Fig. 4. A section of tooth germ cut without decalcification. The free edge of the enamel is splintered, and the boundary line between it and the dentine is dark, the section being deeply stained in this position. × 100.

Fig. 5. Enamel stroma from a similar section cut without decalcification, deeply

- stained with hæmalum. Along its outer border are bodies not capable of being sharply defined, which have stained deeply; then follows a delicate reticulated tissue with distinct longitudinal general arrangement in which are seen oval clear spaces, while below and to the right it merges into a fainter and more open meshed tissue. × 240.

 Fig. 6. A section lying close to the exterior of the apex of a young tooth germ, and cut in a plane transverse to the long axis of the germ about in the position
- and in the plane of the third line across the top of fig. 3. The stained bodies of the exterior of the enamel stroma shown in figs. 3 and 5 are also seen in this, but inside them the whole space is filled up with sharply-bordered rings looking like tubes cut across. × 180.

 Fig. 7. Drawn from a portion of the same section near to its outer portion, though within that which is most deeply stained. The rings surround clear spaces,
- within that which is most deeply stained. The rings surround clear spaces, but these are themselves surrounded by stained areas, the outer edges of which cannot be sharply defined (the definition of the outer edges has been exaggerated in the figure). × 850.

 Fig. 8. Highly-magnified section of enamel stroma which is nearly longitudinal, the
- exaggerated in the figure). × 850.

 Fig. 8. Highly-magnified section of enamel stroma which is nearly longitudinal, the oval form of the sharply-defined areas being due to slight obliquity in the section; they lie in a delicate meshwork, and are the same things as the oval areas seen in fig. 5. × 1000.
- oval areas seen in fig. 5. × 1000.

 Fig. 9. Enamel stroma from a tooth germ in which some enamel has already been calcified. This section having been cut without decalcification, fragments of enamel lie at the bottom of the figure, and above them and between them
- enamel lie at the bottom of the figure, and above them and between them and the unaltered stroma is a more open meshwork. × 180.

 Fig. 10. A portion of young enamel (not decalcified) showing an appearance of tubes
- traversing it. × 300.

 Fig. 11. A portion of enamel seen obliquely so that two surfaces are in view. On its upper surface an appearance of holes, recalling fig. 6, is seen, whilst below
- the side of the fragment is shown. × 240.

 Fig. 12. Enamel of Sheep's-head fish (Sargus) showing the appearance of lines (? tubes) running in from the free surface, and bending and branching till they become lost before reaching the dentine surface (to the right in the figure).